Growth Rates of Atlantic Herring and Atlantic Silverside in Response to Temperature Changes on the Gulf of Maine

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ABSTRACT

As ocean waters warm, it is important to understand how rising temperatures impact marine ecosystems, specifically through the lens of individual organisms and their growth. Atlantic Herring (*Clupea harengus*) and Atlantic Silverside (*Menidia menidia*) are two North Atlantic fish species, which differ greatly in their life cycles and distribution patterns. Silversides have spatial distribution patterns that characterize them as warm-tolerant, while Herring are distributed in a manner that characterizes them as cool-tolerant. Studying how warming waters impact the growth rate of each species could provide valuable information on how climate change will impact different species of fish in the Gulf of Maine. In this study, past data of weekly summer fish lengths in Casco Bay, Maine, were analyzed to derive yearly growth rates of Silverside and Herring. Warm and cool summers were determined from average annual temperature anomalies, which allowed growth rates to be compared across temperature. Atlantic Silverside had faster growth rates in warmer waters, while Atlantic Herring did not show a clear association between temperature and growth rate. This could be due to the migratory nature of Atlantic Herring, and their adaptability to take advantage of many conditions. Better knowledge of how warming waters affect migratory and resident species will be valuable for fisheries management and conservation efforts.

INTRODUCTION

The Gulf of Maine is currently experiencing warming rates faster than 99% of all other ocean ecosystems (Pershing et al., 2015). Casco Bay, a relatively shallow coastal area in the Gulf of Maine, is thus susceptible to some of the fastest warming rates in the world. Warmer waters have a direct impact on aquatic animals through impacts on rates of biochemical reactions and metabolic processes (Little et. al, 2020). Changes in these rates can make larger scale biological processes faster or slower. This can then go on to impact an organisms' overall fitness.

In both laboratory and field studies, some fish have been found to experience higher growth rates in warmer waters (Conover and Present, 1990; Humphrey et al., 2014). However, others have been found to be impacted negatively by warming waters, displaying decreased growth rates with increasing water temperature (Neuheimer et al., 2011). Although these findings are contradictory, some scientists believe that there is a threshold at which warming temperatures no longer benefit a fish, and begin to harm it (Neuheimer et al., 2011). The particular thermal tolerance of any one species is derived from evolutionary adaptation over generations of exposure to the thermal range of their native habitats, one such example being the Red Moki fish (Neuheimer et al., 2011). Red Moki fish from cooler latitudes displayed increased growth rates with increasing temperature in the wild, but those from warmer latitudes had decreased growth rates with increasing temperature in the wild (Neuheimer et al., 2011). This could represent a threshold temperature at which water becomes too warm for fish to handle, and they start to experience decreasing growth rates.

While prior studies focus on how temperature affects one isolated species, this study aims to compare the growth rates of a warm adapted species, Atlantic Silverside, and a cold adapted species, Atlantic Herring, during warmer and cooler summers in Casco Bay. *Menidia menidia (*Atlantic Silverside) and *Clupea harengus (*Atlantic Herring) are native to different latitudes and differ greatly in their life cycles. However, both species are found in the Gulf of Maine during summer months. Silversides are a resident species, meaning that they live in the Casco Bay area for all of their lives, close to shore and in estuaries (Bigelow and Schroeder, 1953). Herring, on the other hand, are a migratory species that travel south to the Casco Bay area from colder waters (Bigelow and Schroeder, 1953). Atlantic Silversides live for 1 to 2 years, while Atlantic Herring can live up to 15 years (Bigelow and Schroeder, 1953). The two species also differ in size. Silversides are smaller, about 6 inches when fully grown, while Herring can grow up to 16 inches in length (Bigelow and Schroeder, 1953). These differences in life cycle, physical features, and native habitat could impact how rapidly the different species could adapt to grow in higher temperatures.

The Gulf of Maine Research Institute (GMRI), in partnership with Quahog Bay Conservancy (QBC), completes a summer seine survey in Casco Bay called the Casco Bay Aquatic Systems Survey (CBASS). Weekly beach seines are conducted to monitor the species that are present, the abundance of these species, and the lengths of individual fish. Based on prior CBASS data from the Gulf of Maine Research Institute, it is known that in cooler summers Atlantic Herring are the most abundant fish in Casco Bay, while in warmer summers Atlantic Silversides are most abundant (GMRI, 2023). This could be an indicator that Silversides have a higher threshold for warmer water temperatures than Herring. Further, prior studies of Atlantic Silversides native to different latitudes have shown that Silversides respond to warming water temperatures with faster growth rates (Conover and Present, 1990). However, Silversides native to colder latitudes had a larger increase in growth rate than those native to warmer latitudes when exposed to the same higher water temperature (Conover and Present, 1990). Silversides native to colder waters need to take advantage of the short warm seasons they typically experience, and respond to warmer waters with significant increases in growth rate (Conover and Present, 1990).

With prior knowledge of the Silversides' ability to adjust its growth rate to take advantage of a warmer period, it is expected that Silversides in Casco Bay will have higher growth rates during warmer summers. Due to Herring being native to cooler waters, it is unknown if they will have a positive growth rate response to warmer summers. The small size and short life cycle of the Silverside explains why it needs to take advantage of warmer seasons, which the Herring may not be as adapted to do. Owing to the fact that Herring are more abundant in cooler summers, it is possible that they will display a negative growth rate response to warming waters. The findings of this study can be useful for the scientific community, as well as fisheries managers, to predict changes in ecosystem health and structure as the Gulf of Maine warms.

METHODS

To collect CBASS data, knotless, delta mesh seine nets (3/16" sq. mesh, 8ft. deep, 150ft. long, with bag) are set at 18 beach sites around Casco Bay each week using a boat (Figure 1). At each site, the end of the net is held at the beach by one person. The boat then backs up while the net is slowly unfolded into the water. When the net is unfolded to the point of the bag in the middle, the bag is put into the water and the boat loops back to shore to drop the other end of the net off at the beach with a second person to hold it. Once the net is set correctly and checked for snags, the people on the beach each pull their ends into shore at the same speed. They pull from the floats on the top of the net and leave the leadline on the bottom. When the net is pulled to the point of the bag, the bag is left partially in the water to keep the fish inside alive. The people onshore pull the leadline from the bottom of the bag up to ensure that no fish can escape. Fish are sorted out of the net one by one, their species identified, and measured for length on a measuring board. The lengths of the first 25 fish for each species at each site are recorded, and individual fish after 25 are tallied but not measured.

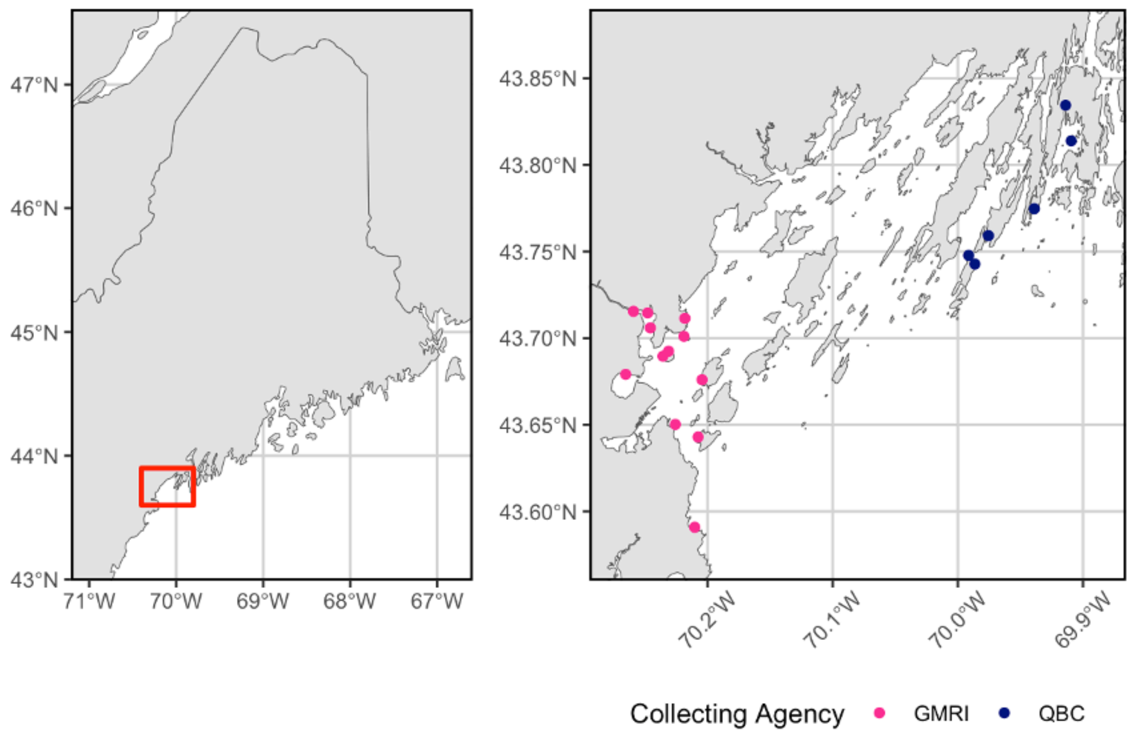

Figure 1. Map of CBASS seine sites in Casco Bay.

This project uses CBASS data from the summers of 2014 through 2023, excluding 2019 due to data collection errors. Data was first cleaned to include only Atlantic Herring and Atlantic Silverside. Data was filtered using mixed distribution modeling to include only the youngest sampled cohorts of fish. This was done so as to not skew calculations with older fish who are plateauing in growth. There was one identified cohort of Herring in each year. Some years had two separately identified cohorts of Silverside, while some only had one.

Temperature data was sourced from the Portland Harbor Tide Gauge, which is run by the National Oceanographic and Atmospheric Administration (NOAA). Data was filtered to include only years 2003-2020 as a climate reference period. Six-minute temperature intervals were averaged over each hour to find mean hourly temperature. This was then averaged to find mean daily temperature for each day of each year. Next, this was smoothed using a general additive model to find normal daily temperature. The smoothed average mean daily temperature was compared to the actual mean daily temperature of years 2014-2023. Average annual temperature anomalies were calculated to determine which years were "warm" and which were "cool."

A generalized linear regression was run on each species in both warm and cool summers to derive growth rates (as average millimeters grown per week) based on weekly length frequency data. It was found that the length data was not normally distributed due to inequality of variance. There was more variability in length towards the end of each summer so a weighted least squares model was run to account for this. This weighted model was then used to derive growth rates. A paired t-test was performed to compare the growth rates of each species in warm versus cool summers. All statistical analysis was performed using R software (R Core Team, 2024).

RESULTS

After calculating yearly average temperature anomalies, it was found that years 2016, 2020, 2021, 2023 and 2022 were warm summers, and years 2014, 2015, 2017, 2018 and 2019 were cool summers (Figure 2; Table 1).

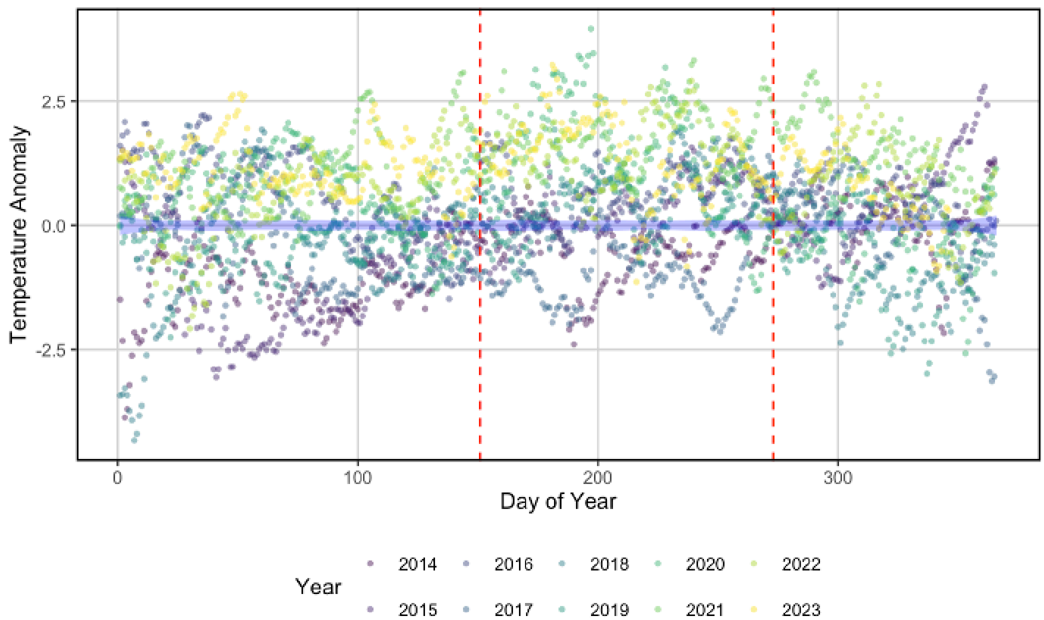

Figure 2. Mean daily temperature anomalies in each year (points) colored by year. The shaded blue region represents a 95% confidence interval around modeled mean temperature anomaly for the climate reference period (2003-2020). Red lines mark the beginning and end of the summer season.

Year	Average Annual Anomaly
2021	1.33
2023	1.14
2022	0.92
2020	0.72
2016	0.58
2018	-0.12
2019	-0.26
2015	-0.27
2017	-0.44
2014	-0.62

Table 1. Average annual temperature anomaly (°C) for each year in comparison to the mean temperature pattern.

Growth rates derived from general linear modeling show that Atlantic Silversides have their 5 highest growth rates in warm summers and 4 lowest growth rates in cool summers (Table 2). Atlantic Herring have their 5 highest growth rates in 2 cool summers and 3 warm summers, and their 4 lowest growth rates in 2 cool summers and 2 warm summers (Table 3). Silversides have their highest growth rates in warm summers, while there is no clear pattern in Herring growth rates (Figure 3; Figure 4).

Year	Growth	Regime
2022	7.05	warm
2023	6.23	warm
2016	5.18	warm
2020	4.49	warm
2021	4.14	warm
2014	3.89	cool
2017	3.54	cool
2018	3.08	cool
2015	2.51	cool

Table 2. Atlantic Silverside growth rates (mm/week) from highest to lowest in cool and warm summers.

Year	Growth	Regime
2015	5.09	cool
2018	4.68	cool
2020	4.09	warm
2016	3.41	warm
2021	2.98	warm
2014	2.64	cool
2022	1.37	warm
2023	1.18	warm
2017	1.01	cool

Table 3. Atlantic Herring growth rates (mm/week) from highest to lowest in cool and warm summers.

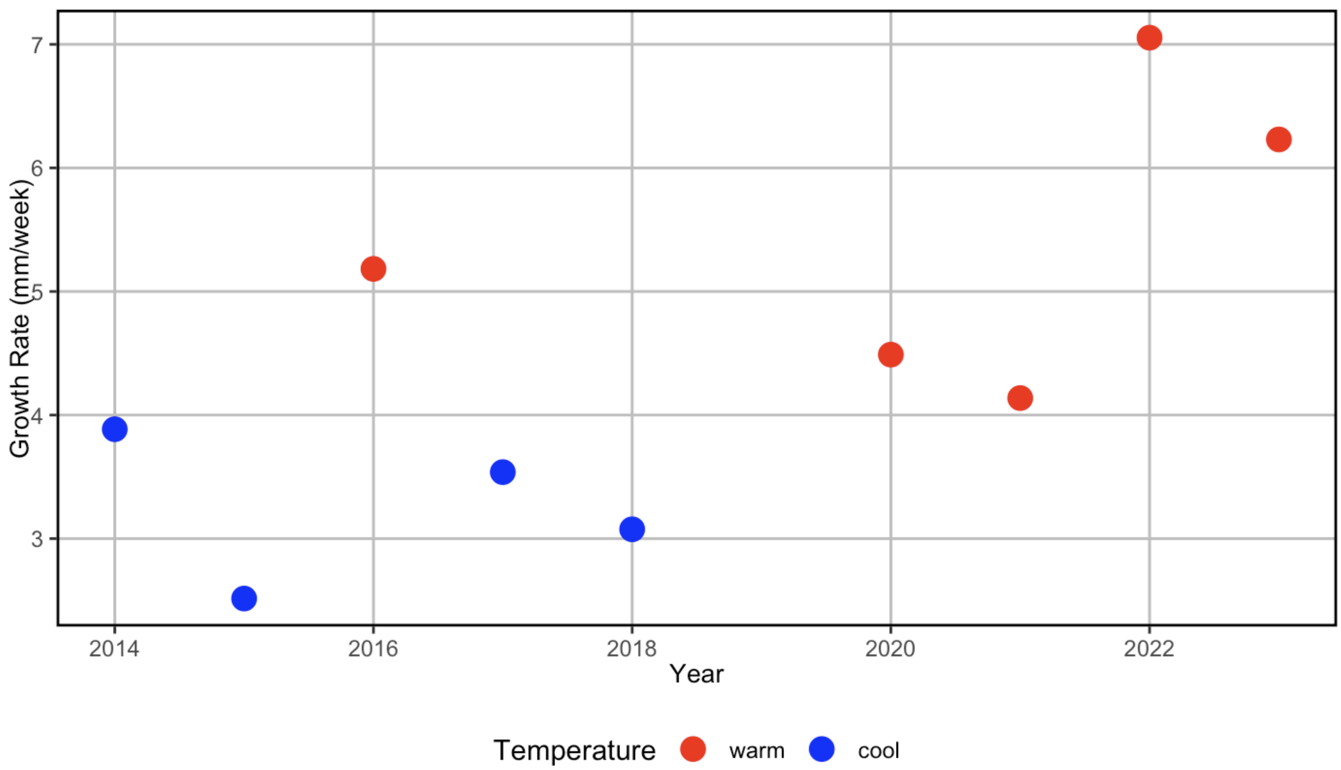

Figure 3. Atlantic Silverside growth rates over time in warm and cool summers.

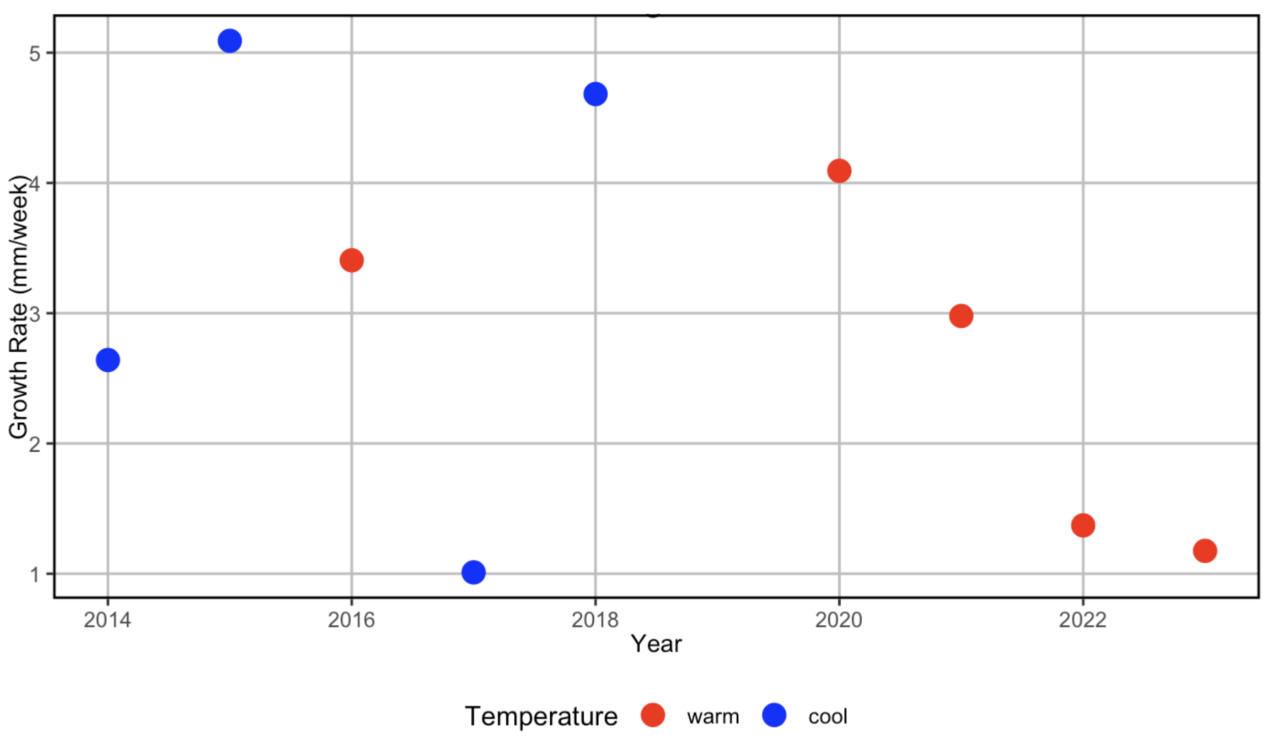

Figure 4. Atlantic Herring growth rates over time in warm and cool summers.

Growth rates are highest in warm years for Atlantic Silverside, and there is no obvious relationship between growth rates and temperature for Atlantic Herring (Figure 5; Figure 6).

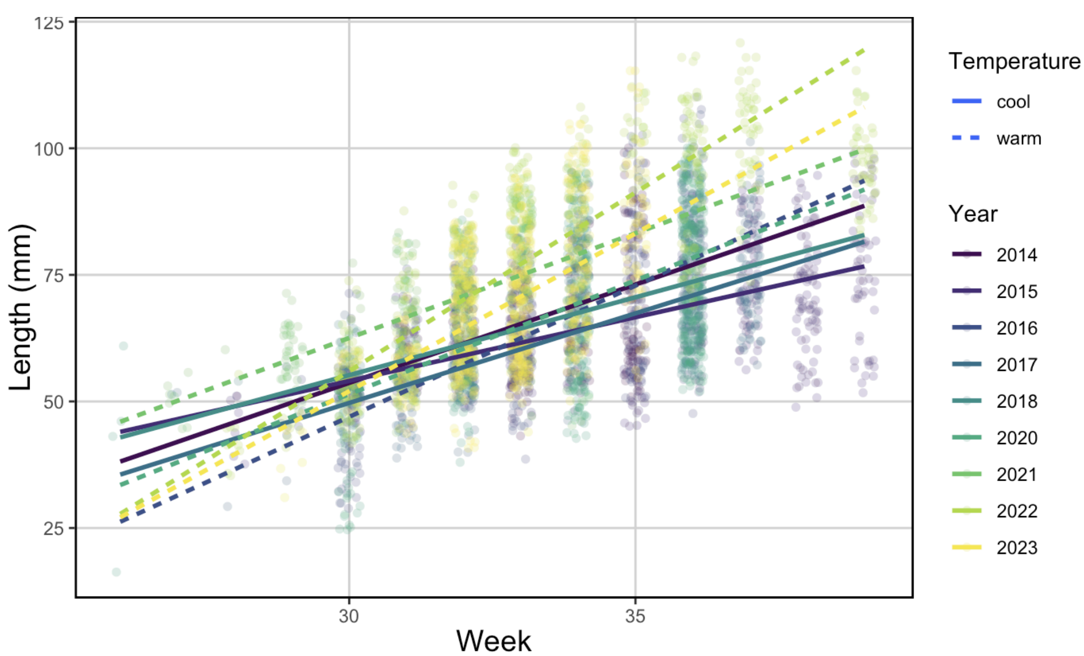

Figure 5. Atlantic Silverside modeled growth rates (lines) over summer data collection weeks. Growth in warm periods is represented by dashed lines, and growth in cool periods is represented by solid lines. Individual fish length measurements are represented as points, with the color of points representing the year of collection.

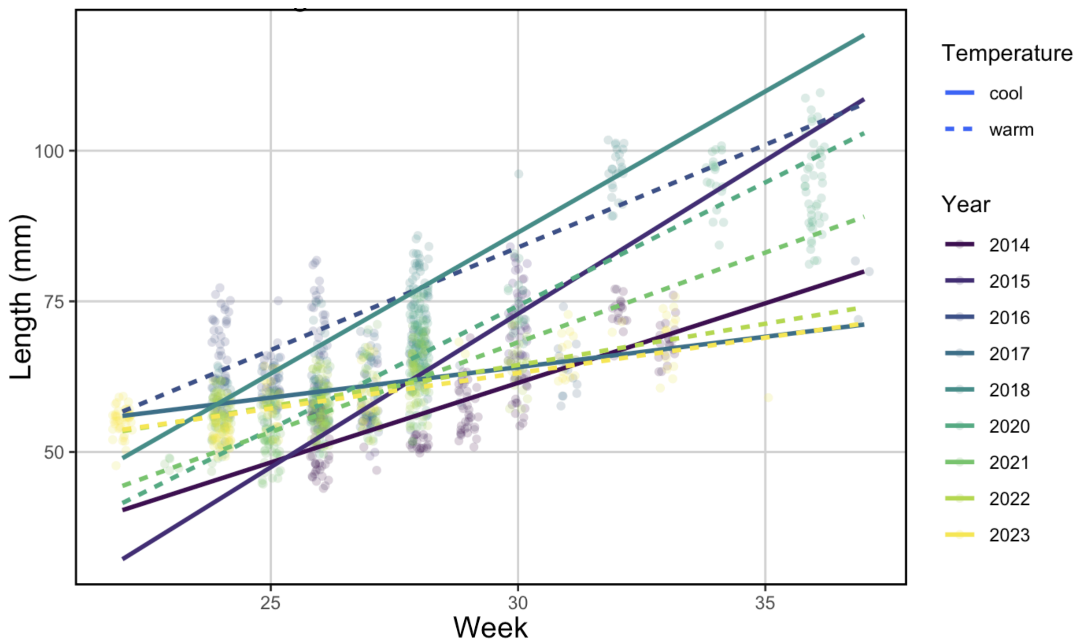

Figure 6. Re-format caption to resemble the one above for silversides

Upon running a paired t-test, it was found that there is a significant difference in Atlantic Silverside growth rates between warm and cool summers (t(6) = 3.50, p= 0.01). A paired t-test found that there was no significant difference in Atlantic Herring growth rates between warm and cool summers (t(5)= -0.678, p=0.53). There is significant overlap in growth rate between warm and cool summers for Herring, while there is no such overlap for Silverside (Figure 7).

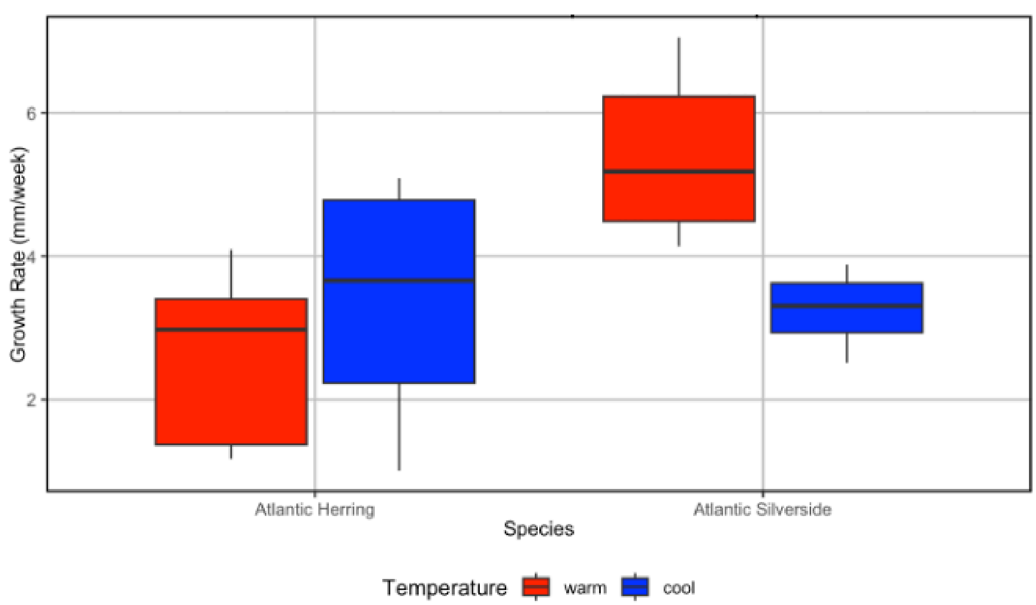

Figure 7. Growth Rate of Atlantic Silverside and Atlantic Herring in warm and cool summers.

DISCUSSION

As predicted, Atlantic Silverside displayed a significant positive correlation between growth rate and temperature. However, Atlantic Herring did not display any significant correlation at all. This could be due to the differences in migration between the species. In the summer months, Herring migrate down the coast to the warmer waters of Casco Bay (Bigelow and Schroeder, 1953). During this migration, they move through changing water temperatures often (Figure 8), which could be a reason why their growth rates are not as affected by warming temperatures (Nottestad et al., 2007). Herring have been found to be highly tolerant to a wide range of temperatures which they experience during their migration, from cold Arctic waters down to the Gulf of Maine (Nottestad et al., 2007). It is also possible that their growth rates are more highly impacted by environmental conditions in other areas along their migratory pathways, or that their growth rates depend on their aggregate exposure to environmental conditions along migratory pathways as a whole (Sinclair and Iles, 1985). The rate and direction of anthropogenic-influenced sea surface temperature changes is spatially variable across the distribution range of Atlantic Herring (Figure 8: Figure 9). Temperature fluctuations in a small area like Casco Bay might not have a clear relationship to derived growth rates because Herring only use Casco Bay for a short period each year, or because the temperature changes in Casco Bay are not representative of the average temperature changes Herring have experienced across their spatial range (Figure 8).

It is also important to note that growth rates are based on many factors, only one of which is temperature. Food availability, water chemistry, and population density can all impact how fast a fish is able to grow. Water temperature can impact all of these factors. Warmer waters could impact how much prey is available for each species, or what time that food is available. A dangerous phenomenon that could be impacting Herring is called spatiotemporal mismatch (Ferreria et al., 2023). This occurs when changing environmental conditions cause food availability to peak at a different time or place than when the predator needs it. Even though warming waters do not directly correlate to lower growth rates in Herring, the abundance and distribution of their prey could shift. Further studies could look at the distribution and abundance of Herring prey in warm and cool summers to see if warming waters may be impacting Herring in other ways. Studies could also shift away from growth rates and look at Herring spatial distribution, seasonal timing, or abundance to get a better idea of how climate change will impact Herring.

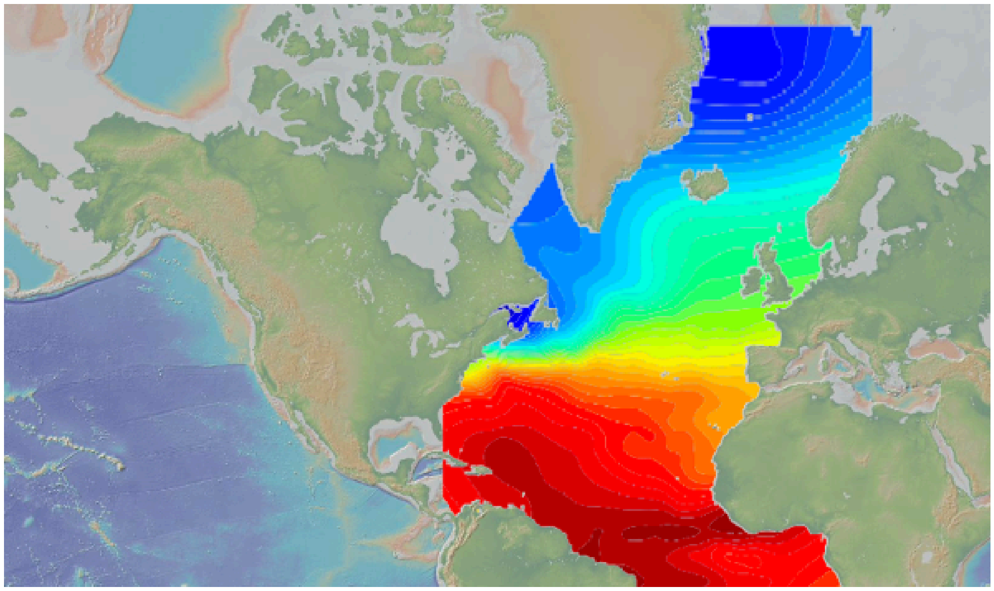

Figure 8. Average Atlantic Ocean surface temperatures in June, red being the warmest and blue being the coldest.

The native ranges of Herring and Silverside differ greatly, with overlap in the Gulf of Maine (Figure 9; Figure 10). Herring, as a whole, are much more present in northern latitudes, while Silversides are found in more southern areas that experience more frequent and intense warming. This could play a role in how well each species is able to adapt to temperature changes. Silversides, who are used to experiencing warmer waters, may be better adapted to take advantage of a warm season. Although Silversides are present down the coast of North America, individual fish do not migrate from where they are born. This means that Silversides experience seasonal temporal changes along Casco Bay, but are only indirectly affected by environmental changes in the wider Gulf of Maine. Herring are subject to environmental changes all up the coast along their migration route, so any Casco Bay specific changes are diluted to them.

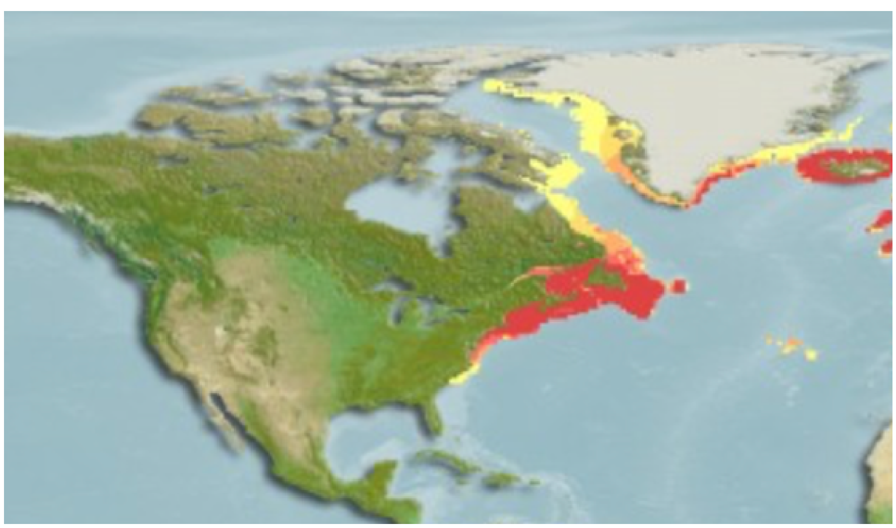

Figure 9. Atlantic Herring distribution pattern, red being the most abundant and yellow being the least abundant (Aquamaps, 2019).

Figure 10. Atlantic Silverside distribution pattern, red being most abundant and yellow being least abundant (Aquamaps, 2019).

This study was based on a smaller than ideal sample size, as it was only over a 10 year period. In order to achieve more robust results, it would be advisable to complete a similar study over a longer period of time. It would also be beneficial to look at years with greater temperature anomalies, which would require a longer time period and warmer seasons. It is also important to note that this study only took place over summers. A year-long study of these fish would provide a more complete picture of their growth, although this would be difficult to achieve due to freezing water and the migration of Herring.

If the trends found in this study continue, it is possible that we will see a shift in the food web from a large presence of cold-adapted fish, such as Herring, to a larger presence of warm-adapted fish, such as Silverside, in Casco Bay. If Silversides are able to take better advantage of the warming waters and grow faster, they could become much more prevalent than Herring, who are not as directly affected by the warming waters. Other warm-adapted species, such as Summer Flounder, may move in as competition to cold-adapted species. Studies found that 23% of Herring recruitment in the North Sea can be explained by plankton abundance (Ferreria et al., 2023). It is possible that shifts in the food abundance during warmer summers could change where Herring migrate, and they could stop coming to Casco Bay altogether. We could see an increase in warm-adapted, smaller, fish, which larger fish like tuna and sharks are not looking to eat. This could greatly shift the food web that currently exists in Casco Bay. Larger fish such as tuna and sharks would be forced to eat more of the smaller, inshore fish, like Silverside, than the larger migratory fish like Herring. This could cause larger migratory fish like tuna and sharks change their eating habits, and perhaps search elsewhere for food. Not only would this create a disruption in the natural ecosystem of Casco Bay, but cause the fisheries which Maine depends on economically to shift as well. Stakeholders in industries which rely on forage fish as well as anyone in fisheries management should pay great attention to shifts in herring behaviors as waters warm. Fishermen as well would be directly impacted by the potential food web shift as a result of warming waters, and should thus be on the forefront of receiving information and pushing for further research and conservation.

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